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MORPHOLOGY AS A FACTOR IN DETERMINING RELATIONSHIPS¹

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The remarkable advance in our knowledge of relationship of organisms during the past quarter of a century is due primarily to extended studies in morphology in one phase or another. In this field data have been gathered from various sources, and there is at present a vast array of recorded observations many of which have been interpreted in terms of relationship and phylogeny. In fact among morphologists and taxonomists relationship and phylogeny have been leading questions of the day. So important is morphology in these matters that it may seem almost axiomatic to speak of morphology as a factor in determining relationships. Nevertheless, the methods of attack have been from such different standpoints and the significance of the results is such that I trust a general statement at this time may not be entirely out of place.

Naturally, I must speak mainly from the standpoint of a taxonomist, and furthermore I shall confine my remarks to a consideration of the higher plants. The general situation as to the morphology of the higher plants, both the gymnosperms and angiosperms, has been so carefully summarized and so admirably presented by Coulter and Chamberlain that no further words are needed to emphasize the importance of modern morphology to a sound taxonomy.

Notwithstanding the amazing progress in modern morphology and the fact that our knowledge of the life-history of individual organisms

¹ Invitation paper read at the symposium on "The Genetic Relationship of Organisms" before the Botanical Society of America at Philadelphia, December 30, 1914.

and genetic relationship of groups of organisms has been materially broadened there has been thus far at least little application of the data obtained to affect, except to amplify, our present system of classification. The basis of classification of the higher plants today is still the old morphology, namely that of Caesalpini, John Ray, Linnaeus, Wolff, Goethe, De Candolle, Eichler, Gray, Bentham and Hooker, and Engler and Prantl; and it is expressed in epitomized form in Engler's *Syllabus der Pflanzenfamilien* (1912), and, so far as the angiosperms are concerned, in a somewhat amplified form by Wernham in recent numbers of *The New Phytologist*. Our present system of classification has resulted from a very gradual development of the science, and along with it there has also developed an elaborate terminology which is more or less arbitrary and to a certain extent fixed. Furthermore, it expresses, as has often been said, the best interpretation of correlated knowledge of relationships up to the time of its publication.

Since the publication of Engler and Prantl's *Die Natürlichen Pflanzenfamilien* morphological research has been directed to various groups of plants a more detailed study of which might throw light upon their genetic relationship. Nowhere has this been more striking than in the Gymnosperms and nowhere I think may it safely be said to have been more effective from a taxonomic standpoint than in this group.

Investigations in plant anatomy have shown conclusively the importance of morphological anatomy in determining genetic relationship or phylogeny. Modern methods, through the work of Scott, Oliver, Arber, Jeffrey, Bailey, Eames, Sinnott and others, have made it possible and profitable to carry on researches along these lines. Morphological considerations of structural elements hitherto unused, or at least used to a very slight extent, have been demonstrated to be of value in determining relationship. How far such characters can be made use of in a general system of classification must remain until a correlation of all facts is effected and possibly for a future generation to decide. Personally, I am inclined to believe that these less obvious features must remain subsidiary to the more evident characters which are relatively easy of access.

There has also been a revival in the study of botanical embryology in its broader aspect, which just at present seems likely to be of the utmost importance in determining finally the relation of monocotyledonous to dicotyledonous plants. In fact morphological evidence is

rapidly accumulating to show that the former group has been derived from the latter. Several writers have expressed this belief, but they have reached their conclusions from rather different points of view. I refer particularly to the recent contributions by Henslow and by Ethel Sargent. Miss Sargent's paper entitled "A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings" points out that "the cotyledon of *Anemarrhena*, a liliaceous genus, contains two massive bundles which together form a tetrarch stele in the primary root"; and she interpreted this as probably due to "a fusion of two seed-leaves in some remote ancestor to form the single cotyledon of *Anemarrhena*." Seedlings of other Liliaceous genera were also examined, but this one she regards as representing a rather primitive type. Miss Sargent contrasts this condition with the condition shown by certain dicotyledonous plants, *e. g.*, species of *Anemone*, *Delphinium*, *Ranunculus*, *Trollius*, *Eranthis*, etc., "possessing seed leaves which are partially united, sometimes by one margin only, but more often by both." The conclusion therefore being that the monocotyledons have been derived from the dicotyledons through a fusion of the two cotyledons into one.

In this connection I may call attention to a very suggestive paper by Coulter and Land in a recent number of *The Botanical Gazette*; they record the results of a morphological study of seedlings of *Agapanthus umbellatus*, a South American amaryllidaceous plant, seedlings of which were found to possess more or less indifferently one or two cotyledons. This study has been continued, and a paper by the same authors was read by Professor Coulter at the recent celebration of the 25th Anniversary of the Missouri Botanical Garden. Although this second paper is not yet published Professor Coulter stated, "The general conclusion is that monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin."

In other words morphological evidence has been presented by Miss Sargent that monocotyledony has resulted by a fusion of two cotyledons and according to Coulter and Land by the reduction and disappearance of one cotyledon. In either case the phenomenon is interpreted as indicating the origin of the monocotyledons from the dicotyledons.

While recent studies have been concerned mainly in determining

the genetic relationship of the larger groups, yet, at the same time, attention has been given to the life history of individual species and groups of species, and to a discussion of the relationship and phylogeny of certain orders, such for example as the *Salicales*, a group recently investigated from an anatomical standpoint by Ruth Holden. This author takes objection to the relatively low position assigned the *Salicales* in the Engler and Prantl system; and she presents anatomical evidence, particularly concerning the primitive condition of the wood—namely vasicentric parenchyma and multiseriate rays—to show that this simple structure is due to reduction. It is interesting to note that in this case at least the anatomical evidence in stem-structure is supplemented by reduction in floral structure and also by entomophilous pollination and porogamy.

Furthermore, it has been maintained, through comparative morphological studies, that the *Fagaceae* have been derived from ancestors allied to epigynous types of *Rosales*; and it is not unlikely, moreover, that a similar genetic relationship may be the case among the *Juglandales*. Several families of plants, for instance the *Araceae* in all probability represent lines of reduction and in this case possibly from some ancestral liliaceous type. It is not inconceivable also that the *Gramineae* may have developed from an ancestral stock allied to the present bamboo tribe. Among the dicotyledonous plants the *Euphorbiaceae* is generally regarded as a polymorphous family in which the floral structure in several genera has been very much reduced, as for example in *Acalypha* and *Euphorbia*.

In such groups as these a more thorough knowledge of the embryology and seedling anatomy would undoubtedly throw light upon genetic relationship as well as generic affinity. I think the objection taken to the relatively low position assigned to several groups in the Engler and Prantl sequence is well founded, but we must wait for additional morphological evidence and its proper correlation before satisfactory change in their position can be made.

Important as these embryological and anatomical studies are in determining genetic relationships, especially of the greater alliances, yet when it comes to a consideration of the relationship of different families and to generic affinity, taxonomy can be materially advanced by a more thorough knowledge of the floras of the different parts of the world. We need also to know more of the life-history of plants already recorded and to have our floras more fully represented in

herbaria and garden. It is my belief that this can be done best through a co-operation of the larger botanical institutions. It is manifestly impossible for any one institution to cover the whole field with any degree of satisfaction, but it is possible for each institution either to direct its energies to a particular territory or to a particular group of plants. Thus it would be possible to place in the hands of the research student an abundance of the necessary kind of material for comparative morphological study and afford the opportunity to determine the range of variability.

Our conception of the origin and limitation of species has been so modified by recent investigations in plant breeding, mutation, hybridization, etc., that relationship in a line of evolutionary sequence is an extremely complex problem. Nevertheless the new morphology, the intensive study of cell-phenomena, and experimental work have done much to advance our knowledge of the relationship of organisms; and it is not improbable that within a comparatively short time we shall have a more complete and satisfactory knowledge of the main phases of phylogeny and the chief lines of evolution of our higher plants.

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